PRESIDENTIAL ADDRESS 1990

Comparative Plant Ecology and the Quest for Understanding of Australian Plants

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(Delivered 28 March 1990)

SYNOPSIS

Understanding the Australian flora involves, firstly, knowing what plants make it up and where they occur, secondly, knowing their origins in geographical and evolutionary terms, and, thirdly, knowing how they inhabit their respective habitats and interact with other components of their environment. The first two sets of knowledge are being addressed on an institutional basis in herbaria across Australia. The third has yet to be tackled in any organized institutional way. It is suggested that this be started, and that attributes of plants be described and compared over all stages of their life cycles to seek relationships between syndromes of plant attributes and ranges of habitats occupied by them.

INTRODUCTION

The discovery by Europeans of eastern Australia and some of its flora occurred in the lifetime of Linnaeus. At a meeting of the Linnean Society of New South Wales, it is thus appropriate to examine briefly directions scientific understanding of Australian plants has taken and might take in future.

The basic question of what plants are in the flora is still being solved. Describing and naming the vascular plants have progressed considerably, but knowledge of non-vascular plants in the flora is scant (see, for instance, Briggs and Leigh, 1988). Much basic taxonomic work remains to be done, simply describing and naming species in our flora.

Questions of origin in Australian plants are being put and being at least partially answered in a geographical sense (see, for instance, Barlow, 1981 and White, 1986) and in the relatedness of plants within groups through cladistic, palaeontological and genomic analyses. Without doubt, such studies will continue to be an adjunct and, to some extent, a spur to basic taxonomic work.

In the course of basic taxonomic work, other kinds of questions are examined. These include distributional questions, principally in a geographical sense but in ecological terms also. Together with work on distributions of individual species, types of vegetation are identified and mapped. Notable pioneering works of this latter sort are those of Beadle (1948) in his mapping and description of the vegetation of western New South Wales and of Costin (1954) in the Monaro.

From patterns of distribution follow questions of why particular species of plants occur where and when they do. It is these questions and closely related ones about their abundance that are ecological. Ways of seeking answers to them are almost as many as there are ecologists, and opinions differ sharply on valid approaches to ecological analysis (see, for instance, Harper, 1982 and Grime, 1984). As Grime (1979) points out, the approaches can be put into three sorts: the correlative, direct and comparative.

The correlative approach seeks to establish correlations between distributions of species and types of vegetation and environmental variation, and uses the correlations to formulate hypotheses about critical factors controlling populations of plants and variation in vegetation.

In the direct approach, essential events in survival and reproduction of individual plants in wild populations are examined and used to find out how the distribution and abundance of plants are controlled in particular populations. It is mostly short-lived herbs that have been studied in this way — see, for example, work reviewed in Harper, 1977. However, some of our local species of woody plants, regeneration of whose individuals or clones is triggered by fire, have also been been studied and some factors controlling their distribution and abundance successfully identified, for example, in *Angophora hispida* (Auld, 1986), *Acacia suaveolens* (Auld, 1987), *Banksia ericifolia* (Bradstock and O'Connell, 1988; Zammit and Westoby, 1988), *B. oblongifolia* (Zammit, 1988; Zammit and Westoby, 1988), *B. serrata* and *Isopogon anemonifolius* (Bradstock and Myerscough, 1988), and *Petrophile pulchella* (Bradstock and O'Connell, 1988).

The comparative approach examines attributes of plants through their life cycles and from them seeks to understand how species of plants occupy specific ranges of habitat. This was attempted in a general way on a world-wide basis by Schimper (1903), but the understanding achieved was necessarily very preliminary and was not based on detailed studies of individual species in a flora. Recently, the Unit of Comparative Plant Ecology in Sheffield, formed on the initiative of Clapham (1956), celebrated 25 years of its existence (Rorison *et al.*, 1987) and published a major compilation and synthesis of its work (Grime *et al.*, 1988). This presents detailed accounts of attributes of some 281 common species of British vascular plants and some details of some 221 other species. It is pertinent to ask whether significant advances in our understanding of Australian plants would be made by such long-term detailed work done on a similar institutional basis to that suggested by Clapham (1956). To do this, it is firstly necessary to outline the essential elements of comparative plant ecology, and then to examine how it has been used in Australia.

The Elements of Comparative Plant Ecology

As in any ecological analysis, the essential elements are environments and organisms. Comparative ecology seeks to handle the ranges of variation in both, and to examine the extent to which particular ranges of attributes of species fit into particular environments.

Environmental variation is mostly handled by some form of classification. Ideally, only physical characteristics of the environment, measured independently of the vegetation, should be used, to avoid circularity in interpreting occurrences of plants in habitats.

With the attributes of plants, all aspects of the life cycle, growth, reproduction, dispersal, germination and establishment, have to be covered. In examining their variation, it is convenient to divide the life cycle into two complementary phases, the regenerative and established phases. This division is common to Grime's system (Grime, 1979; Grime *et al.*, 1988) and to that of Noble and Slatyer (1980). In each system, the regenerative phase covers not only dispersal, germination and establishment through seed or spores, but vegetative re-establishment after loss of leaf canopy and clonal reproduction. The two phases are clearly differentiated in the plant's relationship to resources and mobility. Essentially, on land in the established phase the plant is attached to one place and, if successful, is gathering energy and other resources, increasing its size and

reproductive potential, while in the regenerative phase it is not gathering resources and may be in a form that is dispersed.

Regenerative and established phases of the life cycle are variously related in plants, and this variation is obviously pertinent in variation in occupation of habitats by plants. This can be illustrated by examining four broad types of relationships between seed banks, the dormant, viable seed present, and established plants:

— seed bank ephemeral and growing plants continuously present. This sort of relationship, apparent in many rainforest species, clearly implies an environment in which whole populations of growing plants are not periodically destroyed by disturbance, such as drought, fire, cyclone or clearing.

— seed bank permanent and growing plants ephemeral. This sort of relationship, characteristic in plants of periodically disturbed habitats, is apparent in a whole suite of species in the flora of central Australia.

— seed bank and growing plants both continuously present. This type of relationship occurs in many herbaceous species of temperate grasslands.

— neither seed bank nor growing plants continuously present. This occurs in some species of plants which occur where water is available on a strictly seasonal basis, e.g. *Sorghum intrans* in northern Australia (Andrew and Mott, 1983), and in some species in vegetation that is burnt from time to time, for example *Banksia ericifolia* in vegetation on sandstones in the Sydney region (Siddiqi *et al.*, 1976; Bradstock and Myerscough, 1981; and Zammit and Westoby, 1987).

To provide some basis for comparison for what has been and might be attempted in Australia in comparative plant ecology, it is useful to outline what the Unit of Comparative Plant Ecology in Sheffield has done. In the full summary of the work (Grime *et al.*, 1988) attributes of 281 species of British vascular plants are compared. Central to this comparison is a three-cornered ordering of the species on their attributes taken from all stages of the life cycle. The three extreme syndromes of attributes, strategies in the terminology of Grime (1974), against which each species is ordered, are, in terms of the attributes most useful in identifying them (see Table 3.3, pp. 23, 24, of Grime *et al.*, 1988):

— competitive: shoots with extensive lateral spread and rapidly-ascending dense canopy of leaves in a monolayer with well-defined peaks of leaf production coincident with periods of maximum potential productivity; photosynthetic products and mineral nutrients rapidly incorporated into vegetative structure but a proportion stored for growth in next growing season; potentially high mean relative growth rates.

— stress-tolerant: long-lived plants with evergreen, often small or leathery leaves and long-lived roots and intermittent flowering and often persistent juveniles; low palatability to unspecialized herbivores; potential mean relative rates always low.

— ruderal: very short-lived plants of small stature and limited lateral spread, flowering early in their life-history and devoting a high proportion of annual production to seeds; potentially high mean relative growth rates.

The three extremes approximate, in the system of Southwood and Greenslade (Southwood, 1988), to K-, adversity- and r-selected species respectively. Most species fall somewhere between the three extremes in their syndromes of attributes. In terms of habitats occupied, plants with ruderal syndromes occupy those disturbed frequently, and plants with competitive syndromes those not disturbed and in which resources are freely available, while plants with stress-tolerating syndromes occupy habitats which are not disturbed but are short of one or more resources for plant growth. According to Grime (1977), should frequent disturbance cease in a habitat, the ruderal plants initially

present are replaced firstly by those with competitive syndromes and finally, as resources for plant growth become short, by plants with stress-tolerating syndromes.

Use of Comparative Plant Ecology in Australia

In Australia, Rogers (1988) used the system of Grime (1979), with its triangular ordination of syndromes of plant attributes, in a study of lichens on a palm trunk in Brisbane. He estimated relative growth rates and other attributes of the species of lichens studied and used them to draw axes in triangular ordinations and place each species at a point in each of the ordinations he drew up and examined. He could age the surfaces on the trunk and show that, in time, species with ruderal syndromes according to his ordinations were replaced by those with competitive syndromes.

Generally the system of Grime and his colleagues has been used little other than by him and his colleagues in Sheffield. Use of the comparative approach in Australia and elsewhere has been in other ways. It has largely been directed to one of three ends: understanding temporal relationships between species following disturbance in a habitat, especially fires; understanding habitat differentiation between species of plants and types of vegetation; and understanding ecological differences and similarities between species or higher taxonomic groups of plants.

Temporal Relations Between Species

The system of Noble and Slatyer (1977; 1980), using broad categories of plants in both regenerative and established phases of their life cycles, is largely directed to understanding temporal changes in vegetation following disturbance, especially fire. Their categories in modes of regeneration of plants are closely related to those of Gill (1981) — see Noble (1981). Their system has mostly been used to model changes in temperate forests under various regimes of disturbance. The models proposed require testing, and details of the regenerative and established phases in some of the plants on which the models are based also require confirming.

Habitat Differentiation Between Species

Appreciation of differences between habitats and of general differences of plant attributes between broad classes of habitat has long been characteristic of plant ecology in Australia. In the moist climate of eastern Australia, the difference between rainforest and sclerophyllous vegetation and its relationship to habitat have been explored in the work of Beadle (1954; 1962; 1966; 1968). Within rainforest, variation in leaf characteristics with habitat was clearly shown in Webb's work (1959). As Specht (1970) points out, Diels (1906) drew attention to the variation of hardness of leaves with habitat, leading to the use of the term 'sclerophyll' in the description of certain types of vegetation in Australia.

Leaves are probably one of several plant attributes that vary with habitat. For instance, it is apparent that as soil fertility decreases the proportions of species with serotinous fruits and of those with seeds bearing elaiosomes increase (Milewski and Bond, 1982; Westoby *et al.*, 1982), while the proportion of species with large fleshy fruits decreases, as the vegetation becomes more sclerophyllous and heathy (see, for instance, Milewski and Bond, 1982). It is clear that systematic study of attributes of plants in both their regenerative and established phases in any climatic regime would lead to greater understanding of how various suites of species occupy different parts of gradients of soil fertility.

Ecological Differentiation Between Species or Groups of Species

Comparisons between species over all stages of their life cycles have been made to

understand both their occupancy of different habitats and their co-existence in certain other habitats — see, for instance, Williams' (1979) comparison of *Atriplex vesicaria* and *Maireana pyramidata*. Wider comparison has been made by Noble (1989) between two eucalypt subgenera, *Monocalyptus* and *Symphyomyrtus*. Although it is necessarily based on sketchy and scattered data, it shows that general differences in attributes between the subgenera may explain, among other aspects of ecological differentiation, the frequent co-existence of species of the two subgenera in various types of vegetation. It is clear that comparison of pairs of species or of larger groups of species is one way in which some understanding of both differentiation between species in occupancy of habitat and mechanisms of co-existence in the same habitat may be achieved.

PROSPECTS FOR USE OF COMPARATIVE PLANT ECOLOGY IN AUSTRALIA

Understanding of Australian plants can be greatly increased by systematic work in comparative plant ecology, and the sorts of studies of habitats and attributes of plants required for this can be suggested.

Habitats

Climatic variation is a major consideration in Australian habitats. Major differences of temporal and spatial patterns occur between vegetation of areas where rainfall is usually adequate for plant growth in many months of most years and that of semi-arid and arid areas where moisture is available irregularly for very variable periods. In arid and semi-arid areas, biomass and the relative contributions of particular species in it may vary over several orders of magnitude with amount and season of rainfall — see, for example, Robertson (1987). Conversely in areas where rainfall is greater and more reliable, biomass and the relative contributions of particular species to it vary much less with variation of rainfall in time.

Within climatic zones, site characteristics vary, including soil fertility — see, for instance, Nix (1981). In freely draining sites in both arid and humid areas there is variation of vegetation with fertility. For instance, in arid areas as the clay content of soils declines and they become sandier or rockier there is an increase in xeromorphic grasses of *Triodia*, *Plectrachne* or *Xerochloa* spp. present in the vegetation (Beadle, 1981).

Clearly, if systematic studies in comparative plant ecology were to be undertaken in an extensive way in Australia, seeking relationships between plant attributes and habitat characteristics, a treatment of habitat characteristics would be required that would be independent of the vegetation present in given sites. Such independent treatment could be achieved in terms of some physical characteristics of sites but would be less easily achieved for nutrients and other chemical characteristics in soils due to plant-soil interactions. Any classification of habitats needed almost certainly would be firstly by climatic zones and then by specific site characteristics.

Plant Attributes

Established Phase

Established plants take up energy and other resources. Their attributes are thus likely to be related to availability of resources, both at the shoot and the root.

Stance of leaves appears to be primarily related to availability of water and control of temperatures within tissues, but has secondary implications in productivity of canopies of leaves. Australia is a continent that has dried out relatively recently in geological terms, and it lacks the large succulent-stemmed plants found in some of the drier regions of both New and Old Worlds. Leaves of many longer-lived plants of Australia's arid and semi-arid areas tend to hold their flattened surfaces vertically rather than

horizontally. Such a stance facilitates the transfer of sensible heat to the atmosphere when water is unavailable for significant transpiration, and in dry conditions leaves with vertically held surfaces maintain cooler tissues than do similar leaves with horizontally held surfaces (Mooney *et al.*, 1977). In Australia, a predominantly horizontal stance of leaves only occurs in the scattered rainforest of the eastern coast. The vegetation of much of the rest has more nearly vertical displays of leaves.

Vertically held leaf surfaces are not only more streamlined to transfer of sensible heat to the atmosphere than horizontally held leaves they are potentially more efficient in the uptake of carbon dioxide when they are saturated with light and their stomata are fully open (Larcher, 1980). This is probably part of the explanation for very rapid growth in certain eucalypts, such as *Eucalyptus grandis* and *E. pilularis*, which colonize large gaps on moist, fertile sites in the coastal region of northern New South Wales. Their canopies are also multilayered in the sense of Horn (1971) and for this reason also are likely to be highly productive. Conversely, many species of rainforest tree have horizontally held leaves and may have monolayered canopies in Horn's sense, and, as such, grow more slowly than the eucalypts but are more shade-tolerant and eventually may suppress the eucalypts. Such replacement of eucalypts by rainforest species is outlined in the schemes of Noble and Slatyer (1977; 1980). In short, a vertical leaf stance that may be primarily related to control of leaf temperatures under water stress may also be an important component of the rapid growth of certain eucalypts.

Shoot and root characteristics appear to vary across gradients of soil fertility. In the infertile sand of Dark Island Heath, the data of Specht *et al.* (1958) show large proportions of root in the biomass of the plants, about 75%, compared with 20% to 25% in many forests (Rodin and Bazilevich, 1967), indicating that the organs collecting the resources in short supply are highly developed, while Beadle (1966) has argued that the xeromorphism apparent in shoots of plants on infertile soils is functionally related to their sparing use and conservation in live cells of the plants.

In short, there are already some general lines of understanding variation in attributes of established plants in relation to availability of resources. They require further testing, and one way of doing so is by detailed comparative studies of the attributes across wide ranges of species and environments.

Regenerative Phase

In the regenerative phase, general relationships also appear to exist between plant attributes and environmental characteristics, especially along gradients of resource availability.

Soil fertility affects vegetation and the way it responds to fire. Under infertile conditions, litter is not broken down as rapidly as under fertile conditions (see, for instance, Florence and Lamb, 1975), and, being low in nutrients, phosphorus in particular, such litter is more flammable when dry than that of vegetation from fertile sites. In Australia, seed banks of plants in sites of low fertility show many characteristics in their release, dormancy and germination that are closely related to the incidence and types of fires in such sites — see, for instance, Gill (1981).

The size of seeds may show relationships with variation in habitat. In Britain, Salisbury's (1942) work showed a tendency for seed weight to increase with the shadiness of the habitat in which seedlings of species normally become established, while, in California, a study by Baker (1972) found a similar tendency for seed weight to increase with dryness of habitat. In Australia, it is possible that seed weight may increase in closely related taxa across gradients of decreasing fertility. Work with *Angophora* species in the Sydney region (Mowatt, 1981; Mowatt and Myerscough, 1983) showed that *A. hispida*, a species confined to infertile sites, had the highest mean seed weight while *A.*

floribunda, a species occurring on better sites, had the least, while mean seed weight of *A. costata* was between them both in seed weight and occupancy of sites on a gradient of fertility. A recent study of *Chionochloa* species in New Zealand (Lee and Fenner, 1989) has also shown a similar converse variation of seed weight with fertility of sites occupied by the species. It is also possible that seeds of species occurring in infertile sites may contain a higher proportion of mineral nutrients by weight than those of species from more fertile sites. This was not borne out in the study of *Chionochloa* species by Lee and Fenner (1989), but work of Grundon (1972) showed that seeds of Proteaceae taken from Queensland heath had higher proportions by weight of phosphorus than seeds of other species he tested, including some cultivated species. It is clear that possible relations between site fertility and seed weight and content of mineral nutrient require examining across a range of Australian species and habitats.

Variation in seed weight in relation to availability of resources for establishing seedlings, water in species in the Californian flora (Baker, 1972), light in species in the British flora (Salisbury, 1942) and possibly soil nutrients in Australian plants, can be expected where supplies of resources to the developing seedlings have under selection outweighed constraints on seed size imposed by dispersal or predation of seeds or constraints intrinsic to the development of the fruit or seed itself. The relative importance of such contraints under past selection may be assessed after seed weights have been examined across a range of species.

In Australian rainforests, there are frequently significant numbers of persistent seedlings on the forest floor. Such banks of persistent seedlings may be characteristic of a number of rainforest species and may not occur extensively outside rainforest in Australia. The persistence of such seedlings may depend on mycorrhizal associations through which seedlings may obtain sufficient carbon to maintain slow growth under shade that may be close to the compensation point for net photosynthesis for much of the time. Preliminary work with mycorrhizal and non-mycorrhizal seedlings suggests that this may be so in *Ceratopetalum apetalum* (P. A. McGee, personal communication). The persistence of seedlings and its possible relationship with habitat should be examined across a range of species and habitats in Australia.

Questions for Investigation

Questions to be faced in a systematic ecological comparison of attributes of plants in Australia include:

— What sort of classification, or ordering, of habitats would be the most productive basis across which to compare attributes of plants? Part of an answer to this may be to organize habitats according to where they lie along gradients of soil fertility and drainage within specific climatic zones.

— Are syndromes of attributes of plants likely to be of characteristic types within particular sets of habitats? Preliminary evidence certainly suggests that this is so, both with variation in soil fertility, as indicated above, and with variation in soil drainage. Marked physiological differences appear to exist in the established phase of plants between those that occur in waterlogged habitats and those that do not.

— Can syndromes of attributes be used to predict temporal and spatial relationships between plants? The work of Noble and Slatyer (1977; 1980) indicates that temporal relations may be predicted and could be tested in some situations. Coexistence of species may also be analyzed in terms of attributes of plants and environmental variation in space and time — for instance, see Yen and Myerscough (1989a, b).

— How may syndromes of attributes of various species be profitably classified or ordered? The triangular ordination of Grime (1974) is probably not what is required initially. It is within a confined framework, a framework which carries with it a large amount of interpretation. Initially, some form of open-ended classification, perhaps based on the classes of syndromes of Noble and Slatyer (1977; 1980), would probably be much more useful.

— Are specific sorts of syndromes of plant attributes linked not only to particular ranges of habitat but associated with particular types of breeding system? This sort of question was pursued by Heslop-Harrison (1964) and Baker and Stebbins (1965).

LIMITS OF COMPARATIVE ECOLOGY

Comparison of syndromes of attributes of plants, though highly useful in understanding occupancy of habitats and temporal relations of plants, can not conclusively reveal significant interactions that underlie their patterns of distribution and dispersal. These can only be properly investigated by direct means of careful experimental work in the field (Harper, 1982). Ecological understanding of plants may be best achieved through a combination of the comparative and direct approaches, the first providing both the context and hypotheses for the detailed experimental work in the field of the second.

CONTRIBUTIONS OF COMPARATIVE PLANT ECOLOGY TO OTHER BOTANICAL DISCIPLINES

Contributions of comparative plant ecology are relevant in at least two other areas. Firstly, it is relevant in management of plant populations. In relation to fire, Bradstock and Auld (1987) seek what they term 'indicator species', species characteristic of particular syndromes of attributes and which are either particularly slow or rapid to pass through certain stages of their life cycle, to study reaction of their plants to various aspects of burning in both humid and more arid vegetation. Recognition of such 'indicator species' is clearly an important contribution of comparative plant ecology. More generally, knowledge of syndromes of species may be vital in ecological restorative work in the next century. Such work might include making wildlife corridors to link otherwise isolated nature reserves or national parks, as suggested in a recent submission of the Society on coastal development (Linnean Society of New South Wales, 1990).

Secondly, in gathering data on attributes of plants over the whole life cycle, comparative plant ecology could provide information not only relevant to understanding ecological distributions of species but also useful in taxonomy, allowing alpha-taxonomy to progress toward omega-taxonomy in the sense of Turrill (1938).

CONCLUSION

Botanical understanding is progressing from the basic question of what plants are in the Australian flora to questions of origins of the plants. Beyond these questions are questions of how the plants fit into environments, questions of control of their distribution and abundance. As Clapham (1956) argued, comparative plant ecology can make a tremendous contribution in bringing answers to such questions, especially if pursued on an institutional basis, geared to the long-term goal of finding out in an organized way the attributes of the plants over both the regenerative and established phases of their life cycles.

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